THE OLDEST AMMONOID 'COLOUR' PATTERNS: DESCRIPTION, COMPARISON WITH *NAUTILUS*, AND IMPLICATIONS

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ABSTRACT. Twelve Lower Triassic ammonoid specimens that retain four different 'colour' patterns are described. These 'colour' patterns are the oldest known for ammonoids; three genera (*Dieneroceras*, *Prosphingites*, and *Owenites*) are represented. Four factors contribute to the conclusion that these 'colour' patterns were deposited at the time of growth: (1) the transverse bands are bilaterally symmetrical; (2) the coloration is confined to the outer layer of the test; (3) the pattern is disrupted by sublethal damage to the conch; and (4) the 'colour' is observable through the *Runzelschicht* and is present under the dorsal shell. The ammonoid 'colour' patterns differ from modern *Nautilus* by being present through the terminal growth stage and by being concordant with the growth lines; *Nautilus* loses the colour banding at maturity and has a discordant relationship of colour patterns with growth lines. The transverse 'colour' patterns on ammonoids appear to be less sophisticated than those observed in *Nautilus*; this suggests that the colour patterns on ammonoids may have served a different primary function than that of camouflage.

'COLOUR' pattern preservation on the conchs of fossil cephalopods is a rare phenomenon. Even when the shell survives the processes of fossilization in excellent condition, including the retention of aragonite, the *original* coloration is never preserved. Therefore, detection of 'colour' patterns on fossil cephalopods is dependent on the recognition of consistent non-random patterns of pigmentation expressed in shades of brown or grey that are interpreted to reflect the original colour pattern (Teichert 1964). Reports of such patterns on ammonoids are rare.

'Colour' patterns on nautiloids (Gordon 1964; Teichert 1964; Windle 1973) and bactritoids (Mapes 1979) are known from localities that have co-occurring ammonoids; however, there are currently no Palaeozoic occurrences of ammonoid 'colour' patterns reported. Mesozoic ammonoid examples are limited to twelve reports from widely distributed localities in Europe, North America, and Japan. Cretaceous ammonoid 'colour' patterns include *Tetragonites* (Tanabe and Kanie 1979), *Protexanites* (Matsumoto and Hirano 1976; Tanabe and Kanie 1979), and *Paratexanites* (Matsumoto and Hirano 1976). Jurassic occurrences include *Amaltheus* (Wright 1881; Schindewolf 1928; Spath 1935; Arkell 1957; Pinna 1972), *Androgynoceras* (Spath 1935; Arkell 1957), *Arietites* (Greppin 1898), *Asteroceras* (Arkell 1957; Manley 1977), *Leioceras* (Greppin 1898; Arkell 1957), *Pleuroceras* (Arkell 1957; Pinna 1972), and *Tragophylloceras* (Arkell 1957). The oldest reported occurrence of an ammonoid 'colour' pattern is on a Lower Triassic specimen of *Owenites koeneni* from Nevada (Tozer 1972).

Recent examination of a collection of ammonoids from the same Nevada locality that yielded the specimen described by Tozer, revealed additional specimens of *Owenites* with two distinctly different types of 'colour' patterns. Additionally, distinctly different patterns of relict pigmentation were detected on specimens of *Prosphingites* and *Dieneroceras*.

In this paper we analyse these oldest-known fossil 'colour' patterns on ammonoids and compare them with the true colour patterns on modern *Nautilus*.

LOCALITY AND REPOSITORY

According to Kummel and Steele (1962), the outcrop which yielded this collection of ammonoids is in the *Meekoceras gracilitus* Zone (Lower Triassic), which is exposed in the SW1/4, SW1/4, sec. 34
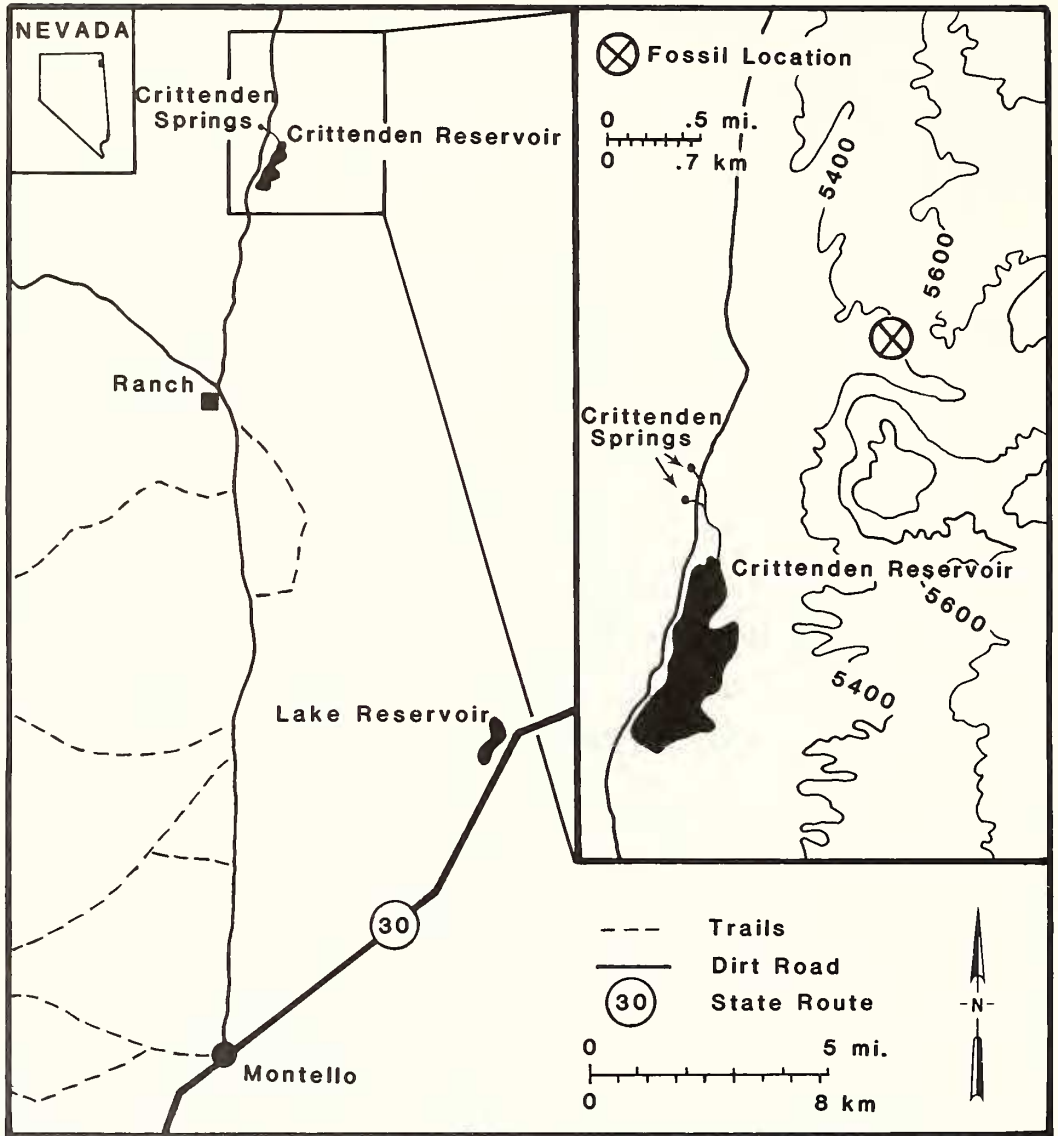
TEXT-FIG. 1. Locality map showing the location of the Crittenden Springs Triassic ammonoid locality in Nevada.

and the W1/2, SW1/4, sec. 3; T.42N., R.69E. (Dairy Valley 15′ Quadrangle). This locality is approximately 1·2 km (1·0 mile) north-east of Crittenden Springs, Elko County, Nevada (text-fig. 1).

Ammonoids are extremely common and typically well preserved at the Crittenden Springs locality. Of the specimens collected, approximately one in 500 retains remnant 'colour' patterns (E. Noble, pers. comm.).

All of the specimens described in this report are reposited at the Department of Geology, University of Iowa, Iowa City, Iowa.

MATERIAL AND DESCRIPTION

'Colour' patterns were observed on twelve specimens. Most specimens retain part of the body chamber; but all save one are missing the aperture. Some have an incomplete test due to mechanical exfoliation produced by cracking out the specimens from the enclosing limestone. Other specimens have weathered surfaces; where this occurs, the alteration appears to have obliterated any trace of remnant 'colour' patterns on the conch.

On the Triassic ammonoid with the 'colour' pattern described by Tozer (1972), pigmentation is found in the 'outer layer of test', and as he pointed out, the 'outer test' also contains growth lines and ornament. These three morphological features are located in the porcelaneous ostracum of *Nautilus* that is secreted by the apertural edge of the mantle. Examination of natural breaks on the twelve newly discovered specimens show that the 'colour' pattern is also confined to the outer layer of the test.

TABLE 1. Measurements (in millimetres) of 'colour' pattern bearing specimens of *Dieneroceras*, *Prosphingites*, and *Owenites* from Lower Triassic sediments at Crittenden Springs, Nevada. An asterisk indicates an estimated measurement.

Specimen	Diameter	Umax	Height	Width
Dieneroceras spathi				
SUI 49171	27·9	9·3*	11·2	5·6*
Prosphingites slossi				
SUI 52308	24·7	8·6	10·0	15·0
SUI 52316	19·6	7·7	9·05	11·5
SUI 52317	18·1	8·0	7·8	12·1
SUI 52318	16·8	5·6	7·1	10·8
Owenites cf. *koeneni*				
SUI 52309	34·0*	6·5	13·8	10·9
SUI 52310	19·6	4·2	8·7	9·1
SUI 52311	25·3	6·1	12·0	10·5
SUI 52312	37·8*	12·6*	18·4	15·1*
SUI 52313	35·5	7·7	14·5	12·9
Owenites sp.				
SUI 52314	37·0	9·9	17·8	12·9
SUI 52315	34·0	6·3	16·1	12·2

The 'colour' pattern on *Prosphingites slossi* consists of continuous, radial bands which extend symmetrically from the umbilical seam across the venter to the opposite umbilical seam (Pl. 42, figs. 1–3). This pattern is present on four specimens (SUI 52309, 52316–52318) (Table 1; Pl. 42, figs. 1–5). On specimen SUI 52308 the venter is enclosed in matrix, and approximately half of the outer whorl can be interpreted as missing because remnants of test are present on the umbilical seam on the preceding whorl. The 'colour' pattern conforms to shallow constrictions in the test which have an average spacing of 1·3 mm. *Runzelschicht* is present on part of the conch, and the pigmentation is faintly discernible under this shell layer. The remaining three specimens have a similar but fainter colour pattern.

The 'colour' pattern on *Dieneroceras spathi* (SUI 49171) consists of a dark greyish-brown longitudinal band on the venter and a dark-grey longitudinal band at the umbilical seam. Faint medium-grey transverse bands are present on the ribs located on the umbilical and lateral region of the conch (Pl. 42, fig. 4). These transverse bands connect with the longitudinal bands at the umbilical seam and on the venter. Only one side of the specimen is exposed; the other side is covered with matrix. Because of this, the bilateral symmetry of the pattern cannot be confirmed (Table 1).
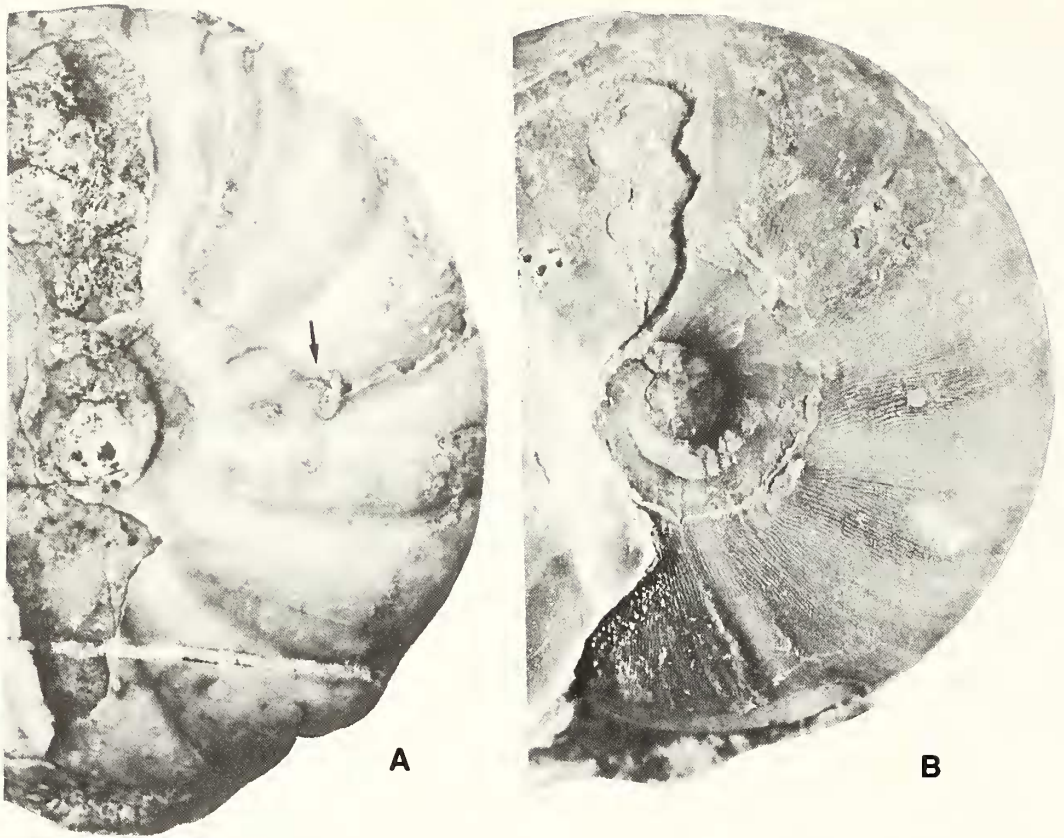
TEXT-FIG. 2. Disruption of 'colour' pattern and *Runzelschicht* on *Owenites* cf. *koeneni*. A, SUI 52313 showing a massive repaired break that interrupts and somewhat offsets the transverse 'colour' bands on the lateral part of the conch (see arrow), × 3·2. B, SUI 52311 lightly coated with ammonium chloride to enhance the *Runzelschicht* layer, × 4·6; the colour pattern on this specimen, which can be observed faintly through the *Runzelschicht*, is more clearly shown on Plate 42, figs. 10 and 11.

Part of the body chamber is missing on this specimen. In this area, dorsal shell is exposed, and where this shell layer is missing on the venter, the greyish-brown longitudinal band is present.

Two different patterns are present on *Owenites*. The most frequently occurring pattern in the collection is that on *Owenites* cf. *koeneni* (SUI 52309–52313) where the shading consists of simple transverse dark-grey bands that cross the venter and disappear on the umbilical lateral part of the conch (Pl. 42, figs. 8–15; text-fig. 2A, B). The 'colour' bands coincide with shallow constrictions and

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EXPLANATION OF PLATE 42

Figs. 1–15. 'Colour' patterns exhibited on *Prosphingites slossi*, *Dieneroceras spathi*, and *Owenites*. All are photographed under xylene to enhance the colour pattern. 1–3, *P. slossi* (SUI 52308), left, ventral, and right sides respectively showing transverse 'colour' bands, × 1·2. 4, *D. spathi* (SUI 49171), left side showing longitudinal bands on the venter and umbilical areas and faint transverse bands on ribs, × 1·5. 5 and 6, *Owenites* sp. (SUI 52314) left and right lateral views showing longitudinal lateral band and transverse bands that cross the venter, × 1·4. 7, *Owenites* sp. (SUI 52315) left lateral view showing longitudinal and transverse bands, × 1·5. 8–15, *Owenites* cf. *koeneni* (SUI 52309–523011, 52313) showing transverse 'colour' bands, magnifications are × 1·6, × 1·3, × 1·2, and × 1·5, respectively.

PLATE 42

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MAPES and SNECK, ammonoid colour patterns

are concordant with the growth lines. Two of these specimens (SUI 52309, 52312) are essentially complete and show indications of mature modifications. A third specimen (SUI 52313) may also be a mature specimen based on 'colour' pattern and constriction approximation.

The other 'colour' pattern is on specimens of *Owenites* sp. (SUI 52314, 52315) (Pl. 42, figs. 5–7). The umbilical area has a brownish-grey tone that abruptly changes to a broad dark-grey band in the mid-lateral region of the conch. Radiating ventrally from this dark-grey band are dark-grey transverse stripes that cross the venter. These transverse stripes are confined to shallow constrictions and follow the growth lines (Table 1). The pattern is best preserved on specimen SUI 52315; the bilateral symmetry of the pattern can be observed best on specimen SUI 52314.

Because the specimens assigned to *Owenites* display two distinctly different 'colour' patterns, assignment at the species level is made with reservation. Additional studies of conch morphology and suture patterns are necessary to determine whether the two 'colour' patterns are species specific in *Owenites*, sexual dimorphism within *O. koeneni*, or normal variation within a species of *Owenites*. At this time, we are reluctant to try to resolve this problem because exposing the suture pattern on the specimens would destroy the preserved 'colour' pattern.

DISCUSSION

The colour patterns on the various species of modern *Nautilus* have been illustrated and generally described by numerous investigators (Willey 1902; Stenzel 1964; Cowen *et al.* 1973). At one time, these were considered to be a species level character (see Saunders 1981 for summary). However, more recent detailed observations by Ward *et al.* (1977) indicate that several colour polymorphs of *N. pompilius* are present and these colour pattern variations have no correlation to sex or depth and cannot be used by themselves to determine species in *Nautilus*.

As Cowen *et al.* (1973) indicate, there is little or no correspondence between the bands of reddish-brown pigment and the shell growth lines. The growth lines on mature *Nautilus* outline a pronounced ocular sinus on each side of the conch and a modest hyponomic sinus at the venter. Earlier stages of the ontogeny show the growth line configuration to be similar but not as pronounced. The colour patterns of reddish-brown bands also generally form a sinus on the venter, but on the lateral parts of the conch, the bands commonly cross the growth lines, coalesce, diverge and/or die out. Often in the umbilical region, the conch is a reddish-brown colour; sometimes stripes penetrate into this region giving darker bands of pigmentation on the reddish-brown umbilical area. In all cases, when *Nautilus* nears maturity, the reddish-brown bands fade on the venter and ventrolateral portions of the conch. Thus, this part of the mature conch is a white to cream colour. Notably many specimens retain reddish-brown stripes in the umbilical region during this stage of ontogeny. Some specimens retain these umbilical stripes to the mature aperture; in others these stripes die out, and the terminal part of the conch is without reddish bands but may retain the less pronounced reddish-brown umbilical shading.

The fossil ammonoids from Nevada have colour patterns with differences from those observed in *Nautilus*. Noteworthy in the ammonoids is the coincidence between the growth lines and pigmentation. The growth lines of the Triassic ammonoid specimens are curved adorally outlining a shallow ocular sinus; the radial 'colour' bands always conform to this configuration. Also, when 'colour' is present, the growth lines are generally coarser.

In *Nautilus*, coloration is due to the presence of melanin, a pigment-causing protein. The chemistry of the 'colour' in ammonoids has not been established. Emplacement of metabolic waste material in *Nautilus* has been postulated by Pruvot-Fol (1935); this possibility cannot be ruled out for the Triassic ammonoids.

COLOUR PATTERNS AND MATURE MODIFICATIONS

Many of the mature modifications of *Nautilus* were described by Willey (1902). A more recent summary and some additional features were provided by Davis (1972) and Collins *et al.* (1978). Some of the external mature modifications that occur in the last stages of growth in *Nautilus* include

the cessation of secretion of colour patterns on the ventral and ventrolateral portions of the conch, deepening of the ocular sinuses, a change in coiling rate (i.e. body-chamber contraction and straightening), and expansion of the aperture (males only; this can also be considered a sexually dimorphic character).

Mature modifications have been recognized in fossil ammonoids for more than 100 years; perhaps the most complete list dealing with the morphological changes that occur at or near maturity is provided by Davis (1972). His list of eleven characteristics includes those known to occur in both the fossil cephalopods and Recent *Nautilus*.

The external character that most strongly suggests specimens SUI 52309, 52312, and 52315 were mature or nearing maturity is the change of coiling. Other external characteristics such as apertural expansion and deepening of the ocular sinuses in *Nautilus* cannot be used with confidence in these fossil forms. The development of constrictions can only be used on specimen SUI 52312 which has a partly intact aperture. Lappets cannot be used since the terminal ends of the body chambers are not present on any except specimen SUI 52312 which does not develop this morphological feature.

The 'colour' patterns expressed on the fossil ammonoids are somewhat different from those patterns that are present on *Nautilus*. In the fossil forms the change in coiling suggests the approach of sexual maturity and cessation of shell secretion. However, unlike *Nautilus*, which during terminal growth and/or the approach of sexual maturity, ceases to produce colour patterns on the venter and ventrolateral parts of the conch, the Triassic ammonoids maintain the 'colour' banding pattern to the aperture. In the vicinity of the aperture the distance between the 'colour' bands generally decreases and they become approximated. Although this 'colour' banding approximation cannot be proved to indicate sexual maturity, it is important that all known specimens which exhibit other mature modifications also had approximation of the ultimate constrictions and also of the 'colour' bands.

BREAKAGE AND REPAIR ON COLOUR PATTERNS

Sublethal breakage and subsequent shell regeneration in *Nautilus* is a phenomenon that has only recently received study even though it was originally noted (but not analysed) by Willey (1902, fig. 15). In 1974 *Nautilus* shell regeneration was extensively analysed using scanning electron microscopy by Meenakshi and others. Bond and Saunders (1984) and Bond (1984) discussed sublethal predation in both fossil ammonoids and *Nautilus*. In the latter study, Bond used *Nautilus* as a generalized model and focused on the interruption of growth lines to determine sublethal events. However, the only study to mention injury and associated disruption of colour patterns on *Nautilus* was by Arnold (1985, p. 388).

A brief analysis of about fifty available specimens (mostly juvenile) of *Nautilus* suggests that four types of sublethal damage will alter the colour patterns on repaired shell. The actual reddish-brown colour on the conch is not changed by sublethal damage; in all four types, the change is a product of interruption and/or regeneration of missing shell in the body chamber region of the conch.

In the terminology developed by Bond (1984), the four major types of breaks that interrupt the colour patterns on *Nautilus* are as follows: (1) Massive—removal of relatively large pieces of test; damage may extend from umbilicus to umbilicus; the breaks include V's, crescents, and scallops. Colour interruptions include sudden termination of reddish-brown colour at the break followed by post-predation shell that typically is white or cream colour. In some cases nacreous shell without colour is deposited (or at least not repaired) at the break. Mantle damage may be associated with this type of break; repairs with this type of damage are described under the third type of break (see below). (2) Moderate—damage is less severe than massive but breaks are still in V's, crescents, and scallops; breaks may extend laterally from venter to umbilicus. Colour pattern interruption is the same as previously described under massive breaks; however, the interruptions are usually less pronounced, and many breaks show no appreciable colour interruption. (3) Narrow-piercing—the breaks, when present, were narrow and deep and affected the mantle; lateral test damage is limited in extent. Colour patterns are sometimes profoundly interrupted and the interruption can continue

to terminal growth stages (more than one whorl). Initial post breakage shell deposition is either black organic material or white coloured shell that forms a narrow band. On many specimens the white coloured shell gradually narrows and becomes a lighter reddish-brown shade than the typical transverse colour bands. In some cases the transverse colour bands secreted after the predatory event are offset by this type of trauma. (4) Minor—damage is less pronounced than moderate with only several growth lamellae missing and the breakage extends for only short distances on the conch; breaks can form small scallops, V's or be irregular. Colour pattern interruptions are minor and only take place at the edges of established reddish-brown bands. Frequently, because of the somewhat irregular nature of the reddish-brown patterns laid down on *Nautilus*, the interruption is difficult to detect even though the minor breakage is clearly expressed by the growth-line interruption.

In the Triassic ammonoids from Nevada, four specimens (SUI 52310, 52312, 52313, 52317) show evidence of sublethal breakage with evidence of colour pattern disruption; several of the remaining specimens show sublethal predation but colour pattern disruption is not evident. The disruptions in 'colour' patterns on the Triassic specimens fall into three of the four colour interruption categories observed in *Nautilus*. The only category not represented is the narrow-piercing break.

On specimen SUI 52310, the sublethal damage is confined to a single place on the venter of the conch and is interpreted as moderate. The colour pattern in the vicinity of the break is a typical transverse band that normally would continue across the venter of the conch (text-fig. 2A). However, the breakage spans the width of the 'colour' band, and the colour band terminates abruptly at the break on both sides of the venter. The shell in the repaired break is a distinctly lighter colour tone that is similar to the grey 'colour' found between the darker 'colour' bands.

Two minor sublethal events interrupted normal 'colour' pattern development on specimen SUI 52312. One break is a shallow indentation of the test that involves several growth lines on the lateral position of the conch. The 'colour' pattern interruption is a decrease in width of the dark transverse band at the position of the break (text-fig. 3B). The adjacent dark bands apicad and orad of the break do not show this decrease in width. The other 'colour' pattern interruption is located more orad on the conch and is a V-shaped notch on the venter. The notch occurs at the orad edge of the dark colour band, and at this place the dark band has been removed. The post-trauma shell repair is of the lighter-grey tone typical of that observed between the darker 'colour' bands.

The third specimen (SUI 52313) has a massive sublethal break that extends across the venter to the umbilicus. 'Colour' pattern interruption is restricted to the lateral part of the conch where two dark transverse bands are offset (text-fig. 2C).

The fourth specimen (SUI 52317) also has massive sublethal damage. The 'colour' pattern interruption is minimal since most of the breakage is located between two constrictions that are a uniform shade of grey.

THE RELATIONSHIP OF DORSAL SHELL AND COLOUR PATTERNS

In *Nautilus*, the dorsal shell is composed of the black layer, which is made up of organic material, and a nacreous aragonite layer that covers the black layer and is usually confined to the posterior end of the body chamber. These two shell layers are known to completely cover the colour patterns of the preceding whorl of the conch. Also, these layers are considered to be homologous to the wrinkle layer (or *Runzelschicht*) found in Paleozoic and Mesozoic ammonoids (Stenzel 1964; House 1971; Tozer 1972).

Ten of the Triassic ammonoids from Nevada (SUI 52308–52311, 52314–52318, 49171) are sufficiently broken back (i.e. missing part or all of the body chamber) to expose the wrinkle layer. Of these, five (SUI 52308, 52309, 52314, 52315, 52318) do not have sufficient exposure or quality of preservation to allow evaluation of the underlying 'colour' pattern and wrinkle layer relationship, and one (SUI 52310) is a phragmocone with only a small patch of wrinkle layer preserved—this specimen has a somewhat frosted appearance and the 'colour' pattern is subdued. On specimen SUI 49171, no wrinkle layer is exposed although dorsal shell is present. This shell layer is covered
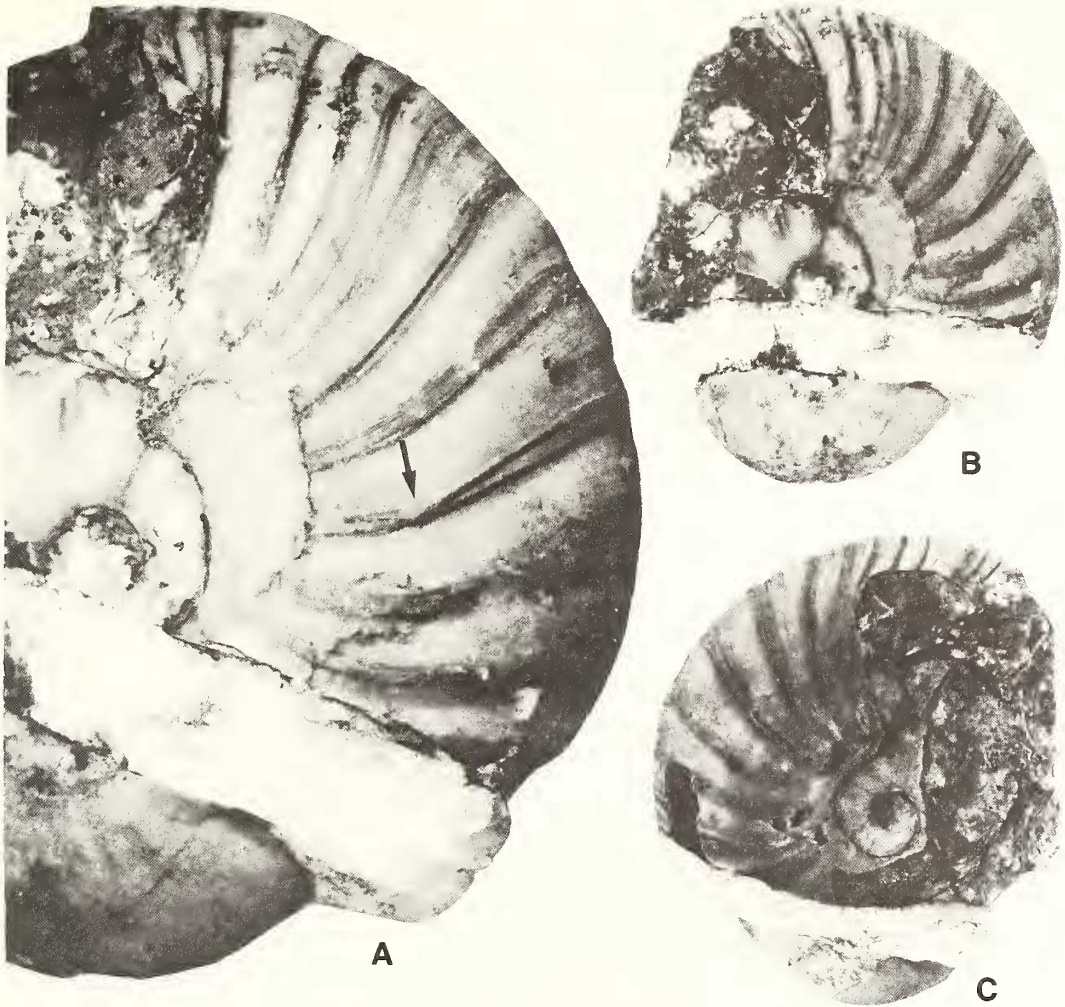
TEXT-FIG. 3. Transverse 'colour' patterns on *Owenites* cf. *koeneni* (SUI 52312). A, Minor sublethal damage on the lateral part of the conch involving several growth lines that causes the 'colour' band to thin (see arrow), × 3·1. B, C, Right and left sides respectively showing the bilateral symmetry of the transverse 'colour' bands, × 1·5.

by a dark organic-looking material that may be equivalent to the black layer in *Nautilus*. Where the dorsal shell has been chipped away, the dark 'colour' band on the venter is preserved. Of the remaining three specimens, one (SUI 52311) is about one-third body chamber which lacks the test and two-thirds phragmocone which is covered with well-developed wrinkle layer (text-fig. 2B). Despite presence of the wrinkle layer, the 'colour' pattern that underlies the wrinkle layer is relatively clearly defined (Pl. 42, figs. 10 and 11). Specimen SUI 52317 is a phragmocone that is also essentially completely covered with wrinkle layer. As with specimen SUI 52310, the 'colour' pattern is clearly exhibited, although the pattern is less pronounced than specimen SUI 52308 which has essentially no exposure of this extra layer of test. Specimen SUI 52316 has a well-exposed wrinkle layer in which the 'colour' pattern does not show through. On this specimen about one-fifth of a whorl has wrinkle layer with two faint constrictions.

CONCLUSIONS AND SPECULATIONS

Crittenden Springs is an important locality because exceptional conditions of preservation have made possible the documentation of a variety of the oldest-known ammonoid 'colour' patterns. Prior comparisons of fossilized cephalopod coloration with that of *Nautilus* may have caused transverse bands conforming to growth lines to be discounted as a relict colour pattern and attributed to a phenomenon of preservation, possibly related to shell density and matrix lithology. Based on these Triassic specimens, we are convinced the colour present is primary, being incorporated at the time of growth. Four factors indicate this: (1) the transverse bands are bilaterally symmetrical; (2) the coloration is confined to the outer layer of test; (3) the pattern is disrupted by sublethal damage to the conch; and (4) the colour is observable through *Runzelschicht* and/or dorsal shell.

Based on examination of the four 'colour' patterns described herein, differences in pigmentation between Triassic ammonoids and modern *Nautilus* become apparent. While the ammonoid specimens retain an approximately regular pattern through maturity, adult *Nautilus* loses pigmentation at a genetically predetermined time of growth so that the terminal ventral surface of the conch is white. Also, the transverse 'colour' banding of the ammonoids conforms to growth lines and constrictions of the shell, whereas in *Nautilus*, the pattern and growth lines are discordant.

These two factors may indicate a profound difference in function of the colour patterns. For *Nautilus* to construct such an arrangement of colour, secretion of pigmentation must occur at different positions on the aperture with growth. Continuity of colour only exists as a function of a specific preprogramming which also controls the cessation of colour banding with the onset of maturity. The result is that the adult *Nautilus* displays irregular, disruptive coloration when viewed from above or laterally and is without pigment when seen from below. Thus, the animal can be considered as camouflaged in its environment (Cowen *et al.* 1973). The function of ammonoid 'colour' patterns and the method of emplacement are not known. Conformity between coloration, constrictions, and growth lines and their presence throughout life may indicate that either this combination of morphological characteristics was not as sophisticated as in *Nautilus*, or the pigmentation does not have a specific purpose such as camouflage. Previously, when 'colour' patterns have been described on fossilized cephalopods, the patterns have been compared to the pigmentation of *Nautilus*. Although ammonoids and *Nautilus* have biologic similarities, it may not be appropriate to try to force interpretations of ammonoid palaeobiology based on comparisons with living *Nautilus*.

REFERENCES

ARKELL, W. J. 1957. Introduction to Mesozoic Ammonoidea. *In* MOORE, R. C. (ed.). *Treatise on invertebrate paleontology, Part L, Mollusca*, L81–L129, Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas.

ARNOLD, J. M. 1985. Shell growth, trauma and repair as an indicator of life history for *Nautilus*. *Veliger*, **27**, 386–396.

BOND, P. N. 1984. Sublethal predation of upper Mississippian (Chesterian) ammonoids. M.Sc. thesis (unpublished), Bryn Mawr College.

BOND, P. N. and SAUNDERS, W. B. 1984. Evidence of predation in Mississippian ammonoids. *Abstr. Progms, geol. Soc. Amer.* **16**, 126.

COLLINS, D., WESTERMANN, G. E. G. and WARD, P. D. 1978. The mature *Nautilus*: its shell and buoyancy. Ibid. **10**, 382.

COWEN, R., GERTMAN, R. and WIGGETT, G. 1973. Camouflage patterns in *Nautilus*, and their implications for cephalopod paleobiology. *Lethaia*, **6**, 201–213.

DAVIS, R. A. 1972. Mature modification and dimorphism in selected Late Paleozoic ammonoids. *Bull. Am. Paleont.* **62**, 130 pp.

GORDON, M. 1964 [1965]. Carboniferous cephalopods of Arkansas. *Prof. Pap. U.S. geol. Surv.* **460**, 322 pp.

GREPPIN, E. 1898. Description des fossiles du Bajocien supérieur des environs de Bale. *Mém. Soc. paléont. Suisse*, **25**, 1–52.

HOUSE, M. R. 1971. The goniatite wrinkle-layer. *Smithson. Contrib. Paleobiol.* **3**, 23–32.

KUMMEL, B. and STEELE, G. 1962. Ammonites from the *Meekoceras gracilitus* Zone at Crittenden Spring, Elko County, Nevada. *J. Paleont.* **36**, 638–703.

MANLEY, C. E. 1977. Unusual pattern preservation in a Liassic ammonite from Dorset. *Palaeontology*, **20**, 913–916.

MAPES, R. H. 1979. Carboniferous and Permian Bactritoidea (Cephalopoda) in North America. *Paleont. Contr. Univ. Kans.* **64**, 75 pp.

MATSUMOTO, T. and HIRANO, H. 1976. Colour patterns in some Cretaceous ammonites from Hokkaido. *Trans. Proc. palaeont. Soc. Japan*, (N.S.) **102**, 334–342.

MEENAKSHI, V. R., MARTIN, A. W. and WILBUR, K. M. 1974. Shell repair in *Nautilus macromphalus. Marine Biol.* **27**, 27–35.

PINNA, G. 1972. Prezenza di trace di coloure sul guiscio di alcune ammoniti della famiglia Amalthidea Hyatt 1877. *Atti. Soc. ital. Sci. nat.* **113**, 193–200.

PRUVOT-FOL, A. 1935. Remarques sur le Nautile. *Int. Congr. Zool.* **3**, 1652–1663. Twelfth session, Lisboa.

SAUNDERS, W. B. 1981. The species of living *Nautilus* and their distribution. *Veliger*, **24**, 8–17.

SCHINDEWOLF, O. H. 1928. Über Farbstreifen bei *Amaltheus* (*Paltopleuroceras*) *spinatus* (Brug.). *Paläont. Z.* **10**, 136–143.

SPATH, L. F. 1935. On colour markings in ammonites. *Ann. Mag. nat. Hist.*, ser. 10, **15**, 395–398.

STENZEL, H. B. 1964. Living *Nautilus*. *In* MOORE, R. C. (ed.). *Treatise on invertebrate paleontology, Part K, Mollusca*, K59–K93. Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas.

TANABE, K. and KANIE, Y. 1979. Colour markings in two species of tetragonitid ammonites from the Upper Cretaceous of Hokkaido, Japan. *Sci. Rep. Yokosuka Cy Mus.* **25**, 1–6.

TEICHERT, C. 1964. Morphology of hard parts. *In* MOORE, R. C. (ed.). *Treatise on invertebrate paleontology, Part K, Mollusca*, K13–K53. Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas.

TOZER, E. T. 1972. Observations on the shell structure of Triassic ammonoids. *Palaeontology*, **15**, 637–654.

WARD, P. D., STONE, R., WESTERMANN, G. and MARTIN, A. 1977. Notes on animal weight, cameral fluids, swimming speed, and colour polymorphism of the cephalopod *Nautilus pompilius* in the Fiji Islands. Ibid. **3**, 377–388.

WILLEY, A. 1902. Contribution to the natural history of the pearly nautilus. *Zoological results based on material from New Britain, New Guinea, Loyalty Islands and elsewhere, collected during the years 1895, 1896 and 1897. Part 6*, 691–803. Cambridge University Press, Cambridge, England.

WINDLE, D. L. 1973. Studies in Carboniferous nautiloids: cyrtocones and annulate orthocones. Ph.D. thesis (unpublished), University of Iowa.

WRIGHT, T. 1881. Monograph on the Lias ammonites of the British Islands. *Palaeontogr. Soc.* [*Monogr.*], **4**, 205–328.

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